

AN EXPERIMENTAL FIELD STUDY OF THE FUNCTION OF CRESTED AUKLET FEATHER ODOR

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Abstract. During the breeding season, female and male Crested Auklets (*Aethia cristatella*; Alcidae) emit a pungent citruslike odor from their plumage. Previous experiments showed that captive birds oriented toward sources of the natural odor and toward isolates of its major constituents, cis-4 decenal and octanal, and avoided a noxious odor. In a blind experiment we manipulated odor on 12 life-sized, realistic Crested Auklet models (6 males, 6 females) to test for a social or sexual preference for the odor isolates in a natural setting. Based on the quantified behavior of 555 males and 280 females that approached the models at a breeding colony, we found no evidence for a sexual preference for models with added odor. Female auklets that approached male models with artificially added odor were no more likely to perform sexual displays than females that approached control models with less odor. Fewer males approached female models but the effect was the same: males that approached female models with artificially added odor were no more likely to perform sexual displays. However, males approached scented male models more closely and for longer duration than they approached control male models, and females approached scented male models more closely. Our findings confirm previous experiments with captive birds and further suggest that Crested Auklets' plumage odor serves at least a general social function.

Key words: *Aethia cristatella*, Alcidae, chemical communication, Crested Auklet, plumage odor, sexual selection, social signal.

Estudio Experimental de Campo de la Función del Olor de las Plumas en *Aethia cristatella*

Resumen. Durante la estación reproductiva, el plumaje del macho y la hembra de *Aethia cristatella* (Alcidae) emite un olor picante-cítrico. Experimentos previos han demostrado que las aves en cautiverio se orientan hacia fuentes de olor natural y hacia extractos de sus principales constituyentes, cis-4 decano y octano, y evitan un olor nocivo. En un experimento a ciegas, manipulamos el olor en 12 modelos de tamaño real de *A. cristatella* (6 machos y 6 hembras) para probar la preferencia sexual o social por los extractos en un ambiente natural. Basados en el comportamiento cuantitativo de 555 machos y 280 hembras que se acercaron a los modelos en la colonia reproductiva, no encontramos ninguna evidencia por una preferencia sexual por los modelos con el olor añadido. Las hembras de *A. cristatella* que se aproximaron a los modelos con el olor artificial añadido no presentaron una probabilidad mayor de realizar despliegues sexuales que las hembras que se acercaron a modelos con poco olor (control). Sin embargo, los machos se acercaron más y por más tiempo a los modelos de macho con olor que a los modelos de macho control, y las hembras se acercaron más a los modelos de macho con olor. Nuestros resultados confirman experimentos previos en aves en cautiverio y sugieren que el olor del plumaje de *A. cristatella* tiene por lo menos una función social general.

INTRODUCTION

Social odors, usually defined as intraspecific chemical stimuli that alter behavior or physiology, usually through olfaction (Johnston 2000), have been well described from most classes of vertebrates. In some species, odors function in

mate choice and may be favored by intersexual selection (Andersson 1994). However, few data on the function of social odors are available from birds, though every bird species that has been examined closely has a functioning sense of smell (Roper 1999). Furthermore, plumage odors noticeable to human observers are also fairly widespread among birds, with evidence from 177 species, 80 genera, and 19 orders (summarized by Weldon and Rappole 1997). Nevertheless, few studies have addressed the so-

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cial function of avian plumage odor. Studies of captive Mallards (*Anas platyrhynchos*; Balthazart and Schoffeniels 1979, Jacob et al. 1979) provided evidence for changes in male sexual behavior correlated with seasonal variation in uropygial gland chemistry of females. A recent experimental study of captive Crested Auklets (*Aethia cristatella*) demonstrated orientation in a maze toward their unusual tangerine-scented feather odor, and also toward an artificial mixture of two seasonally elevated chemical components of their feather odor (Hagelin et al. 2003). Field experiments on the social function of avian plumage odors are needed to confirm odor's role in chemical communication.

Here we describe an experimental field study designed to examine the social role of plumage odor in Crested Auklets. Auklets (family Alcidae) are socially monogamous, sexually monomorphic seabirds in which males and females display ornaments only during the breeding season (Gaston and Jones 1998, Jones et al. 2000). In addition to the tangerine-scented odor, the function of which is unclear, Crested Auklets have a sexually selected forehead crest composed of black, forward-curving feathers (Jones and Hunter 1993, 1998), less conspicuous white auricular plumes, and a brilliant orange bill with elaborate curved accessory plates. The distinctive citruslike plumage odor is readily detectable to human observers at breeding colonies and near flocks at sea (Humphrey 1958, Jones 1993a, 1999, Hunter and Jones 1999, Jones et al. 2000). Chemical constituents of the plumage odor include octanal, cis-4-decenal, hexanoic acid, and a variety of related compounds (Douglas et al. 2001, Hagelin et al. 2003). Although the maze experiments performed by Hagelin et al. (2003) demonstrated preferential orientation toward feather odor and its chemical constituents, they were not designed to test for a social function of the odor *per se*. Apart from any other evidence, the social function of the odor is suggested by Crested Auklet courtship behavior involving extensive exploration with the bill of the nape and other strongly scented areas, including one particularly conspicuous display referred to as "ruff-sniffing" (Jones 1993a, Hagelin et al. 2003).

Crested Auklet courtship, mate choice, intra-sexual conflict, and territorial disputes for nesting crevices take place at colonies prior to laying (involving pairs breeding in the same year), and

throughout the remainder of the breeding season (for breeding in subsequent years see Jones 1993a). Copulation takes place on the sea near the colony (Hunter and Jones 1999).

Mating preferences for, and social functions of, auklet feather ornaments have been previously tested experimentally by using manipulations of ornament size on realistic taxidermic models positioned on display rocks in auklet colonies (Jones and Montgomerie 1992, Jones and Hunter 1993, 1998, 1999). Auklets initially approach this type of model as in natural encounters, and display both courtship and agonistic behavior to the models. This approach offers an ideal method to experimentally test for the social significance of plumage odor.

The objectives of our study were to (1) test for orientation of wild Crested Auklet males and females toward conspecific models with added plumage odor, (2) test for an increased frequency of sexual displays (evidence of a mating preference) by males and females toward opposite-sex models with added plumage odor, and (3) generally evaluate the accumulating evidence for various functions and mechanisms for the origin and maintenance of auklet plumage odor.

METHODS

MODEL EXPERIMENTS

To experimentally test whether the Crested Auklet feather odor is attractive for social reasons (e.g., natural selection for an aggregating mechanism) or favored by mating preferences (intersexual selection), we performed manipulation experiments using 12 realistic taxidermic models made from the skins of freshly dead adult Crested Auklets (six males and six females) collected at a very large mixed-species auklet colony at Sirius Point, Kiska Island, Aleutian Islands, Alaska (52°08'N, 177°35'E). The breeding population of this colony was estimated at approximately 650 000 Crested Auklets and more than one million Least Auklets (*Aethia pusilla*; Day et al. 1979). Our experiments were required to test whether plumage odor *per se* and not some correlated aspect of individual phenotype could influence behavior toward scented individuals. We were particularly interested in testing whether mating preferences might favor the odor. We compared the response of approaching auklets to each of two different odor levels: a control model without added odor, and

a treatment model with supplemental synthetic chemical scent. The models of each sex were similar but differed slightly in natural ornament expression and posture; their natural appearance was enhanced by glass eyes with white irides and orange-painted bills (the natural bright-orange bill color fades rapidly after death). By placing artificial odor on auklet models rather than live birds, we controlled for two factors that could confound the experiment. First, we could measure behavior in a controlled situation (between bird and model), to exclude circumstances when intrasexual interactions involving several individuals were likely to affect individual responses to the ornaments. Furthermore, because we manipulated odor on immobile models, we ensured that birds' responses to manipulations were due to a change in the odor *per se* rather than a change in behavior of a manipulated live bird. Our experimental approach was based on the assumptions that increased sexual displays (see Jones 1993a) and closer approach for a longer duration toward a manipulated model were indicative of a mating or social preference for an opposite-sex model's phenotype (Jones and Hunter 1993, 1999).

We quantified the responses of Crested Auklets to models equipped with identical patches of dark-gray fleece ($5 \times 15 \times 25$ mm) attached to the nape region and held in place with a 25-mm-diameter stainless-steel wire loop around the neck (wire thickness 0.25 mm). Each of the 12 models was assigned two patches, one (odor patch) treated at the beginning of each presentation day with 0.1 mL of a 2:1 mixture of cis-4-decenal (Sigma-Aldrich chemicals, St. Louis, Missouri, order number 375624) and octanal (order number 05608), and the other (control patch) to which no odor chemicals were applied. To simulate the odor, we used the same mixture of stock chemicals previously used by Hagelin et al. (2003) because there is no known method of extracting and distilling natural Crested Auklet odor chemicals from the birds' feathers. This chemical mixture contains the principal and seasonally elevated constituents of Crested Auklet plumage odor, and elicited similar responses to natural feather odor from captive Crested Auklets in maze experiments (Hagelin et al. 2003). Although we do not know whether auklets and humans perceive the odor similarly (e.g., Welton and Rappole 1997), to our noses the smell from the odor patches was similar to that from

napes of live Crested Auklets. At 9°C (the average air temperature during the experiments) evaporation of the odor chemicals from the patch would produce a local odor concentration about 1–4 times that of the natural feather odor from a live Crested Auklet in windless conditions. Odor chemicals were stored in a glass jar between presentation days. Control patches were stored separately in a clean plastic bag to preclude cross-contamination. Natural appearance was maintained by concealing the edges of the patch and the supporting wire under the nape and neck feathers. Each fleece patch had a backing of 0.5-mm-thick plastic to preclude contamination of the model's feathers with odor chemicals from the patch. Each patch was individually marked for identification by model number and odor/control designation on the plastic backing (invisible when the patch was in place). Little natural odor remained on the feathers of the models, because heat applied during the taxidermy drying process caused evaporation of the odor volatiles. Although our experimental design was limited by the effects of wind and evaporation on the odor stimulus during presentations, we believe it provided the best possible opportunity for assessing the attractiveness of Crested Auklet plumage odor.

We presented models at 40 different display rocks (large boulders with 2–12 m² flat upper surfaces, where auklets congregated to court. We presented models daily (excluding periods of precipitation and winds over 20 km hr⁻¹) between 7 June and 14 July 2002 during the incubation and hatching periods, when both breeding and nonbreeding birds court intensively (Jones 1993a). Responses to the 6 male models were scored by ILJ; responses to the 6 female models were scored by HLM. We alternated the presentation of odor and control patches on each model every successive day of presentation, beginning with odor, then control, then odor again, etc. Observer bias was controlled for in the experiment by selecting unambiguous displays for scoring (Jones 1993a), by making simultaneous observation training trials to maximize observer consistency, and by carrying out blind experiments. Each observer quantified auklet responses, using binoculars from a concealed sitting position 30–50 m from the models, to four models at a time. The models in use on any day were selected randomly, with odor and control patches assigned by the other observer. We scored

Errata

Methods Page 73, left column, paragraph 2, lines 6-12

third sentence erroneously reads:

“Each of the models was assigned two patches, one (odor patch) treated at the beginning of each presentation day with 0.1 mL of a **2:1** mixture of cis-4-decenal (Sigma-Aldrich chemicals, St. Louis, Missouri, order number 375624) and octanal (order number 05608), and the other (control patch) to which no odor was applied.”

This sentence was not worded correctly; it should read (**correct version**):

“Each of the models was assigned two patches, one (odor patch) treated at the beginning of each presentation day with 0.1 mL of a **1:2** mixture of cis-4-decenal (Sigma-Aldrich chemicals, St. Louis, Missouri, order number 375624) and octanal (order number 05608), and the other (control patch) to which no odor was applied.”

Note that a 1:2 mixture of cis-4-decenal and octanal was used in the experiment

Discussion Page 76, starting on last line in left column

sentence erroneously reads:

“The experiments were also based on the assumption that our use of the artificial **2:1** mixture of cis-4-decenal and octanal stimulated the same response as natural odor.”

This sentence was not worded correctly; it should read (**correct version**):

“The experiments were also based on the assumption that our use of the artificial **1:2** mixture of cis-4-decenal and octanal stimulated the same response as natural odor.”

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approximately equal numbers of responses for each treatment, so the mean presentation date was similar for each model and each treatment, thereby controlling for seasonal effects.

For each adult Crested Auklet that responded to a model (i.e., approached within 30 cm and at least visually inspected the model) we identified its sex by bill shape (Jones 1993b), and recorded the occurrence of sexual displays (arch, hunch, ruff sniff and touch; see Jones 1993a for detailed descriptions), as well as their closest approach (0, 1–10, 11–20, 21–30 or >30 cm, relative to small measured paint marks placed to the side and front of the models and by comparison to the 20-cm height of the models) and response duration (1–5, 6–10, 11–15 or >15 sec). Auklets respond to models as if they are live birds for at least the first 15 sec following presentation (Jones and Montgomerie 1992, Jones and Hunter 1993, 1999). We believe no individual's response was scored more than once because of the huge number of birds present and because we shifted the models among display rocks frequently.

STATISTICAL ANALYSES

To statistically analyze differences in response between model treatments, we collapsed the data into a single frequency measure for each response behavior for each model for each treatment. To evaluate mating preference and general social attractiveness, we analyzed male and female responses to female models and female and male responses to male models using the frequencies of (1) approaches closer than 10 cm, (2) approaches for longer than 10 sec, and (3) the performance of one or more sexual displays. We separately analyzed responses of subadult Crested Auklets, which cannot be sexed in the field from their appearance (Jones 1993b). We compared responses using paired *t*-tests on arcsine-transformed frequencies of distance of closest approach, duration of approach, and display frequency. Because theory and previous experiments predict that added plumage odor would be more attractive than less odor (Hagelin et al. 2003), we used one-tailed tests to evaluate whether responses (μ) were greater for the models with added odor (i.e., $H_0: \mu \leq 0$ and $H_A: \mu > 0$; see Zar 1984).

RESULTS

RESPONSES TO MODELS

We recorded a total of 1056 responses to models during 119 hr of observation on 17 different days between 17 June and 16 July 2002. We recorded 353 responses to male models with added odor, 342 to male models with no added odor, 179 responses to female models with added odor, and 182 to female models with no added odor. The number of responses varied highly from day to day based on varying levels of auklet activity at the colony and on the display rocks chosen for presentations. The total number of responses to male models (695) was greater than to female models (361) although the duration of presentations was the same for male and female models. The frequency of responses did not differ between odor and control treatments for either male (353:342, binomial $P = 1.0$) or female (179:182, binomial $P = 1.0$) models. However, for males approaching the models with accentuated odor, there was a significantly stronger response to female models compared to male models for proximity of approach ($t_{10} = 5.1$, $P < 0.001$), duration of interest ($t_{10} = 6.2$, $P < 0.001$), and frequency of display ($t_{10} = 2.5$, $P = 0.03$). For females approaching the models with accentuated odor, there was a significantly stronger response to female models compared to male models for duration of interest ($t_{10} = 4.1$, $P = 0.002$), and frequency of display ($t_{10} = 4.1$, $P = 0.002$), but not for proximity of approach ($t_{10} = 0.7$, $P = 0.5$).

RESPONSES TO MALE MODELS

Female auklets that responded to male models approached the scented male models more closely than the control models (Table 1, Fig. 1). However, there was no trend for females' duration of interest. Furthermore, female auklets that approached male models with artificially added odor were no more likely to perform sexual displays compared to male models without added odor (Table 1). Male auklets that responded to male models approached scented models both more closely and for longer duration than they approached control male models (Table 1, Fig. 1). Male auklets did not perform sexual displays toward male models but several birds assumed a distinctive arched posture or performed the trumpeting vocal display while responding to the models (Jones 1993a); there was no difference

TABLE 1. Responses of male, female, and subadult Crested Auklets to male and female models with and without added plumage odor.

	Overall	Control	Odor	Paired t_2	P
Female responses to male models					
Responses scored	400	201	199		
Proximity of approach <10 cm	76	29	47	2.7	0.02*
Duration of interest >10 sec	54	27	27	0.7	0.75
Any sexual display	143	68	75	0.3	0.38
Male responses to male models					
Responses scored	155	71	84		
Proximity of approach <10 cm	29	8	21	2.2	0.04*
Duration of interest >10 sec	25	8	17	2.4	0.03*
Any sexual display	35	16	19	0.2	0.58
Female responses to female models					
Responses scored	118	50	68		
Proximity of approach <10 cm	57	31	26	1.4	0.88
Duration of interest >10 sec	74	26	48	1.6	0.09
Any sexual display	34	20	14	1.4	0.89
Male responses to female models					
Responses scored	162	83	79		
Proximity of approach <10 cm	99	49	50	0.5	0.31
Duration of interest >10 sec	99	46	53	1.8	0.07
Any sexual display	63	30	33	0.7	0.25
Subadult responses to male models					
Responses scored	140	70	70		
Proximity of approach <10 cm	46	24	22	1.7	0.93
Duration of interest >10 sec	45	19	26	1.6	0.09
Any sexual display	68	31	37	0.6	0.30
Subadult responses to female models					
Responses scored	68	41	27		
Proximity of approach <10 cm	37	28	9	0.6	0.71
Duration of interest >10 sec	30	16	14	0.8	0.78
Any sexual display	68	41	27	0.6	0.27

* $P \leq 0.05$.

in frequency of these displays between odor and control models. Considering the proximity-of-approach response category, the response of males to male odor models was no different from the response of females to the same models (test comparing the frequency of approach to within 10 cm between odor and control models, $t_2 = 0.2$, $P = 0.8$). Subadults did not respond statistically differently to male models with added odor (Table 1).

RESPONSES TO FEMALE MODELS

There was no significant difference between either males' or females' approach between control and odor models for duration or closeness of approach (Table 1). Males that approached female models with artificially added odor were not more likely to perform sexual displays. Sub-

adults did not respond statistically differently to female models with added odor compared to control models (Table 1).

DISCUSSION

We elected to use model experiments to evaluate the social function of Crested Auklet plumage odor because previous experiments had successfully manipulated similar realistic auklet models to examine the social function of auklet feather ornaments (Jones and Montgomerie 1992, Jones and Hunter 1993, 1998, 1999). Because we manipulated odor on immobile models, we ensured that auklets' responses were due to a change in the odor *per se* rather than a change in the behavior of manipulated live birds (e.g., Balmford and Thomas 1992). Furthermore, because of the blind experimental design, the results could not

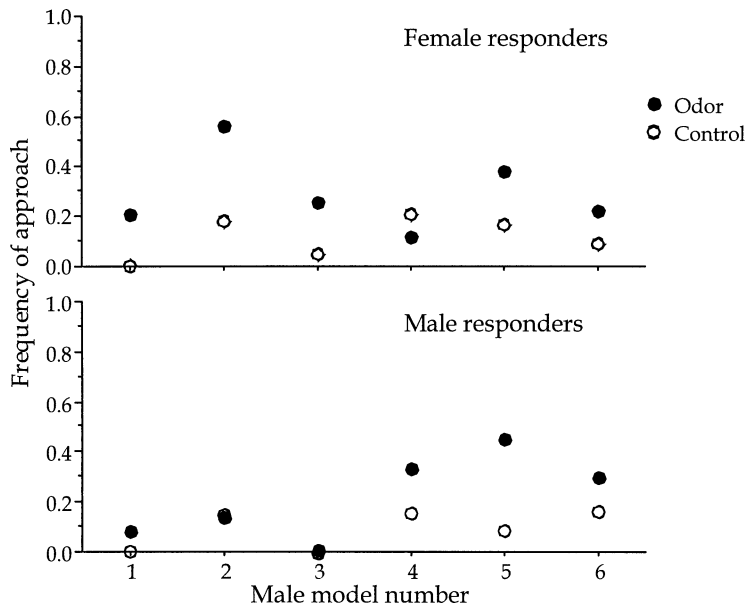


FIGURE 1. The response of male and female Crested Auklets to experimentally altered plumage odor, as measured by frequency of approach to within 10 cm of male taxidermic models presented at a large colony at Kiska Island, Alaska, in 2002.

have been affected by observer bias. Our experimental approach was based on the assumptions that increased sexual displays (see Jones 1993a) would indicate a mating preference for an opposite-sex model's odor, and that closer approach for a longer duration would indicate a social preference for the plumage odor. However, odor was not as easy to experimentally manipulate as a feather ornament. First, due to variable wind speeds and directions close to the models the odor stimulus to approaching live birds could not be precisely controlled and some birds (approaching from upwind) could have approached the model without being exposed to the odor stimulus. Second, evaporation of the 0.1 mL of *cis*-4-decenal and octanal from a cool (ca. 9°C) patch of fleece attached to the models' napes would be expected to produce a different odor compared to evaporation from the warm (ca. 30°C) feathers of a live auklet. Third, our presentations were limited to days with ideal weather conditions (rare in the Aleutian Islands), leading to difficulty in attaining a sufficient sample of responses. Fortunately, these three limitations would tend to reduce the possibility of detecting a response to odor rather than creating a bias that could lead to a false positive conclusion. The experiments were also based on the

assumption that our use of the artificial 2:1 mixture of *cis*-4-decenal and octanal stimulated the same response as natural odor.

Previous experiments using captive Crested Auklets in a maze showed that auklets oriented similarly to natural odor (i.e., volatile compounds emitted from natural feathers) and artificial odor (volatile compounds from a mixture of stock chemicals identified as the primary components of this species' feather odor; Hagelin et al. 2003). Our field experiments were similar in that Crested Auklets were able to detect and orient toward the same artificial odor applied to male (but not female) models presented in a natural setting. Crested Auklet behavior at the colony (Jones 1993a) and on the sea (Hunter and Jones 1999) implicated the odor in social and sexual behavior because closely interacting birds appear to sniff one another's plumage, a possibility requiring experimental confirmation. The experiments resulted in generally closer approach and longer duration of interest to male models with accentuated odor compared with the control models, consistent with the previous maze experiment (Hagelin et al. 2003) in which birds oriented toward an invisible odor source. In our experiments, the effect was statistically significant but not very

strong with some models eliciting a more noticeable difference between odor and control presentations (Fig. 1). We believe this was due to the likelihood that some birds approaching models with odor patches were not exposed to the odor stimulus, for the reasons outlined above. Nevertheless, birds responded to the male models as if they were live birds and their attraction to models with odor was detected.

The most striking differences between this experiment and previous ones using manipulated feather ornaments (e.g., Jones and Hunter 1999) was that the response to odor was only statistically significant for birds approaching male models, and did not involve an increased frequency of sexual displays. Experiments using similar models in which the crest ornament was manipulated showed a twofold increase in sexual displays by males to female models with accentuated crests, and a fourfold increase in sexual displays by females to male models with accentuated crests (Jones and Hunter 1999). No such response was detected for odor. This suggests that Crested Auklet plumage odor may have a more general social function rather than being primarily used as a sexually selected ornament for attracting mates. This is consistent with previous suggestions that the odor helps individuals maintain social cohesion within flocks of this highly gregarious bird at the colony and at sea (Jones 1993a, Douglas et al. 2001). Taken together with the results of Hagelin et al. (2003), our data provide the best available evidence for a social function of odor in any bird species.

It is difficult to imagine how Crested Auklet feather odor could be used, like the striking crest and other visual ornaments, to attract mates from a distance in the windy conditions present on display rocks at colonies. However, our results do not preclude the possibility that Crested Auklet feather odor functions in courtship in very close-range interactions, such as during the ruff-sniff and neck-twist displays, which occur in the more advanced stages of courtship and immediately prior to copulation (Jones 1993a, Hunter and Jones 1999). This possibility was not detectable with our model experiments but might be testable with manipulations of captive birds in an aviary setting. Further experiments and investigations are required to elucidate the physiological and morphological basis of Crested Auklet feather odor production, its use in courtship and pair bonding by established pairs, its

role in flocks at sea, and to test the suggestion that the odor chemicals function for repelling ectoparasites (Douglas et al. 2001).

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